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Intraspecific craniometric variation in a chromosome hybrid zone of *Ctenomys minutus* (Rodentia, Hystricognathi)

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Abstract

Intraspecific craniometric variation in a population of *Ctenomys minutus* (2n = 46, 47, and 48) from a hybrid zone was studied using univariate and multivariate techniques. The study showed greater morphological variation among females than among males. Analysis of populations that contain hybrid forms suggest some degree of morphological divergence among cytotypes.

Key words: *Ctenomys minutus*, hybrid zone, skull morphology

Introduction

Ctenomys is a genus of fossorial rodents endemic to southern South America which comprises about 56 species (Woods 1993). Regarding both morphology and ecology, *Ctenomys* is highly convergent with North American pocket gophers (Geomyidae), Middle Eastern and European mole rats (Spalacidae), and African mole-rats (Bathyergidae) (Nevo 1979). *Ctenomys* species have high karyotypic diversity with diploid numbers varying from 2n = 10 to 70 (Reig et al. 1990).

The four species of *Ctenomys* that occur in the southern Brazilian state of Rio Grande do Sul, are *C. torquatus*, *C. lami*, *C. minutus*, and *C. flamarioni*. They have been reviewed previously (Freitas 1995). *C. minutus* inhabits fields and pastures in the southern Brazilian coastal plain of Rio Grande do Sul and Santa Catarina. In the centre of this distribution a hybrid zone was found with chromosomal numbers varying from 2n = 46 to 2n = 48 (Gava 1996; Freitas 1997).

Hybrid zones of fossorial rodents have been studied in many species from various genera, e. g. *Thomomys* (Thaeler 1974; Patton 1993), *Spalax* (Nevo 1986), and *Ctenomys* (Gava 1996; Freitas 1997).

The aim of this study therefore is to investigate the skull morphological variation in *C. minutus* and ist relation to the chromosomal hybrid zone.

Material and methods

The sample consisted of 108 kariotyped specimens of *Ctenomys minutus* with chromosomal numbers distributed as follows: 53 specimens with 2n = 46 (30 males and 23 females), 8 specimens with 2n = 47 (3 males and 5 females), and 47 specimens with 2n = 48 (25 males and 22 females) (Gava 1996).

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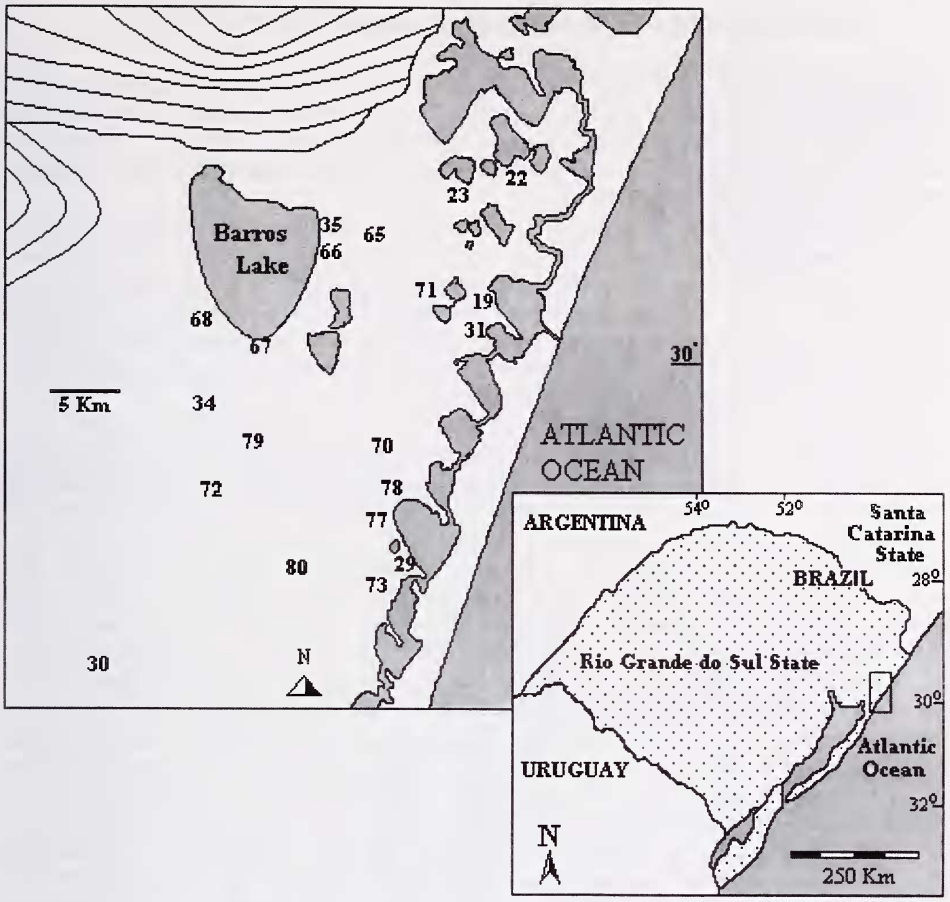

Fig. 1. Map of southeastern Rio Grande do Sul, Brazil, showing the sample localities of *Ctenomys minutus*.

Samples from 18 numbered population localities were plotted on a map of south-eastern Rio Grande do Sul (Fig. 1). The number of individuals by cytotype in each population and the distance between localities were determined by a south-eastern to north-eastern transect, crossing the hybrid zone from locality 30 to locality 22 (Gava 1996).

Eleven standard cranial measurements (Langguth and Abella 1970), in millimeters, were taken as follows: 1) GSL: Greatest skull length, 2) NL: Nasal length, 3) NB: Nasal breadth, 4) BB: Bimeatal breadth, 5) ZYB: Greatest breadth across zygomatic arches, 6) MTB: Greatest breadth across the mastoid, 7) RB: Rostral breadth, 8) POD: Greatest diameter at pre-orbital foramen, 9) DIA: diastema, 10) MSL: Length of molar tooth row, 11) PRL: Length of the palatinum.

All linear measurements were log-transformed to normalise the original measurements. A two-sample t-test was used to evaluate sex-related differences and differences due to variation in chromosomal number ($2n = 46$, 47, and 48). The statistical analysis of skull morphology was made by two methods, first by univariate analysis and secondly by multivariate analysis. Canonical Discriminant Functions Analysis and Principal Components Analysis were used to classify the three cytotypes separately for males and females. Data from the 11 cranial measurements of the 108 specimens were divided into male and female classes and submitted to univariate analysis separately for males and females. All statistical analyses were made using NCSS 6.0 – Number Cruncher Statistical Systems (Hintze 1995).

Results and discussion

The two-sample t-test showed significant differences in 10 measurements, except for MSL between males and females. A t-test was made for each skull characteristic measurement of the three cytotypes (2n = 46, 2n = 47, and 2n = 48) as is shown in table 1. The only significant difference between 2n = 46 and 2n = 48 was for POD, with POD in 2n = 48 greater than in 2n = 46 ($t = 2.911$, $p > 0.05$).

Multivariate analysis is commonly used to determine systematic positions, morphometric variations, and taxonomic relations e. g. in fossorial rodents such as *Geomys personatus* (Williams and Genoways 1981), *Spalax ehrenbergi* (Nevo et al. 1988; Nevo and Beiles 1989), *Geomys tropicalis* (Williams and Genoways 1977), *Geomys arenarius* (Williams and Genoways 1978), *Geomys pinetis* (Williams and Genoways 1980), *Ctenomys dorbignyi* (Contreras and Scolaro 1986), Bolivian species of *Ctenomys* (Cook et al. 1990), and *Ctenomys talarum* (Bush et al. 1989).

The results of multivariate analysis suggest that females had greater variation than males in Principal Components Analysis (Morrison 1976; Chatfield and Collins 1980). The first factor accounted for 67.2% variation and the cumulative percent for the first three factors accounted for 82.8% of the observed variation. In a correlation matrix, the measurements that showed variation in factor 1 were: GSL, BB, ZYB, DIA, NL, POD, and NB respectively. Measurements that showed variation in factor 2 were: PRL, RB, MSL, and MTB, respectively. Males presented 89.9% of variation in factor 1 and 94.8% considering the cumulative variation of the three first factors. All measurements showed variation in factor 1, as follows: GSL, PRL, BB, ZYB, DIA, RB, POD, NB, NL, MTB, and MSL, respectively. The hybrid form, 2n = 47, presents an intermediate position between the parental karyotypes. Analysis of Canonical Discriminant Functions for the three cytotypes, separately for males and females, showed that females are more variable than males, but in both sexes the separation is distinct and the hybrid shows significant variation in the second score, which represents a shape variable. The classification error of females showed a reduction of 64% compared with 56% in males with hybrids in a peripheral position (Fig. 2). Analysis of Canonical Discriminant Functions for populations that present hybrid forms, considering both males and females, presents a classification error reduced to 59.6% but the peripheral position of hybrids is most evident, suggesting some degree of morphological divergence among cytotypes.

Table 1. Skull measurements of three cytotypes of *Ctenomys minutus*. Mean values ± Standard Deviation and sample size (in parenthesis) are given.

	2n = 46 (53)		2n = 47 (8)		2n = 48 (47)	
Meas[a]	Males (30)	Females (23)	Males (3)	Females (5)	Males (25)	Females (22)
GSL	46.5 ± 4.3	43.5 ± 2.5	43 ± 4.5	43 ± 2.2	47 ± 3	43.7 ± 1.8
NL	16.6 ± 1.8	15.8 ± 1.12	15.1 ± 2.7	15 ± 1	16.7 ± 1.1	15.7 ± 0.8
NB	6.7 ± 0.8	6.1 ± 0.5	5.7 ± 0.7	6 ± 0.6	6.9 ± 0.6	6.2 ± 0.4
BB	26.7 ± 2.2	25.4 ± 1.8	24.8 ± 2.6	25.1 ± 1.3	27.2 ± 1.4	25.8 ± 0.9
ZYB	28 ± 2.5	26.1 ± 1.3	25.6 ± 2.8	26.5 ± 1.3	28.6 ± 1.9	26.8 ± 0.8
MTB	25.8 ± 2	24.6 ± 1.2	24.8 ± 2.1	24.3 ± 1	25.9 ± 1.6	24.6 ± 1.3
RB	11.5 ± 1.2	10.4 ± 0.8	10.4 ± 1.1	10.5 ± 0.6	11.7 ± 0.9	10.8 ± 0.4
POD	9.7 ± 1.1	9.1 ± 0.7	8.6 ± 1.4	9.1 ± 0.7	10.2 ± 0.8	9.5 ± 0.5
DIA	13.5 ± 1.6	12.5 ± 0.9	12.2 ± 2.1	11.9 ± 1.1	13.6 ± 1.1	12.5 ± 0.8
MSL	9.4 ± 0.8	9.1 ± 0.6	8.6 ± 1.5	9.4 ± 0.5	9.6 ± 0.6	9.3 ± 0.4
PRL	21.9 ± 2.4	20.4 ± 2.3	19.8 ± 3.3	19.5 ± 1.4	22.1 ± 1.8	20.5 ± 1.1

[a] Measurements. Abbreavations are spelled out in text.

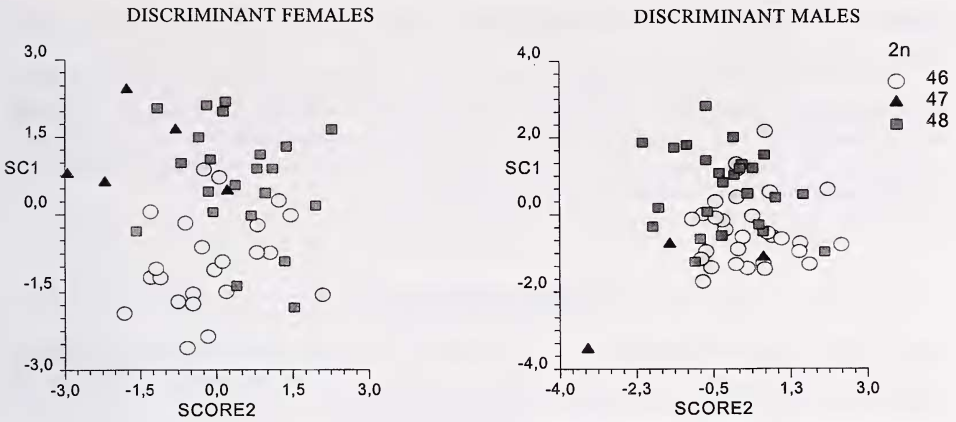

Fig. 2. Comparison of samples of three different cytotypes of *Ctenomys minutus*. The abscissa is the second Discriminant Function and the ordinate is the first Discriminant Function.

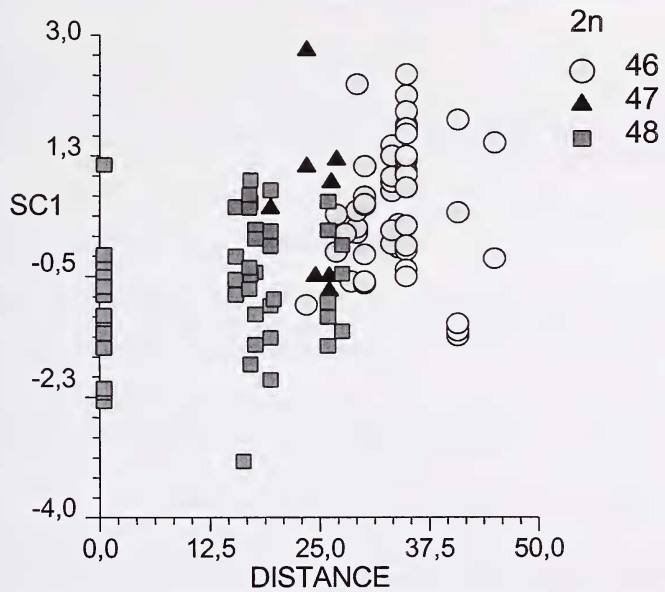

Fig. 3. Individual distribution of first scores of Discriminant Analysis plotted according to transect length among population sites. Distance between populations plotted in a south-eastern to north-

The hybrid zone is approximately 10 km wide (Gava 1996) and the individual scores in Canonical Discriminant Functions were plotted according to the distance in km. Figure 3 shows the variation of the animal scores according to their cytotype in the study area. The position of hybrid forms and a change from negative scores (2n = 48) to positive scores (2n = 46) can be clearly observed.

Despite the cytogenetic difference, the hybrid male meiosis produces a trivalent and, since there is evidence denoting the possibility of balanced segregation and normal fertility in simple Robertsonian heterozygotes, the width of the hybrid zone is a function of

the dispersal capability of each individual and the time since secondary contact (Gava 1996).

The geographic range of *Ctenomys minutus* is accompanied by chromosomal variation and intraspecific craniometric variation, mostly among females. This could be explained by historical factors such as populations having been separated by ancient geographic barriers which no longer exist today thus allowing contact among individuals with different diploid numbers (Villwock and Tomazelli 1995).

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Zusammenfassung

Intraspezifische craniometrische Variation in einer chromosomalen Hybridzone von Ctenomys minutus (Rodentia, Hystricognathi)

Die intraszpezifische craniometrische Variation einer Population von *Ctenomys minutus* aus einer Hybridzone (2n = 46, 47 und 48) wurde mittels univariater und multivariater Methoden untersucht. Es zeigte sich eine größere morphologische Variabilität innerhalb der Weibchen gegenüber den Männchen. Die Analyse von Populationen, die Hybridformen einschließen, belegen ein gewisses Ausmaß morphologischer Divergenz zwischen den Cytotypen.

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